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ROOT SIZE AND SHOOT/ROOT RATIO AS INFLUENCED BY LIGHT ENVIRONMENT OF THE SHOOT

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ABSTRACT: The light environment of a plant shoot can affect its root size and the shoot/root biomass ratio. Photoperiodic influence on shoot/root ratios of first-year biennial sweetclover (*Melilotus alba* Desr.) plants was related to phytochrome measurement of day length and its regulation of photosynthate partitioning to favor successful completion of the life cycle. Short photoperiods alternated with long, uninterrupted nights resulted in low-growing shoots and rapidly enlarging taproots. The ratio of far-red (FR) relative to red (R) light and its effect on shoot/root biomass ratios were studied in controlled environments, in different field population densities, and among plants growing in full sunlight but receiving different spectral distributions of upwardly reflected light over different colored soils, plant residues or artificially colored mulches. Altered spectral distribution of reflected light can act through photomorphogenic pigments within a plant and influence photosynthate partitioning and shoot/root biomass ratio. Application of some basic photobiological principles should lead to improved plant-soil-water-light management in crop production systems.

INTRODUCTION

Roots are of many sizes and shapes, and shoot/root biomass ratios in some species may change dramatically during the life cycle of the plant. The shoot/root relationships are influenced by genetics and the environmental combinations that exist during plant growth. That is, comparison of genetically- identical seedlings under different growth environments shows that the plant with the largest shoot may or may not have the largest root system, depending on environmental conditions.

The "strategy" of each plant is to sense the total growth environment, and invest only enough carbon in roots to support the plant as it proceeds through its life cycle. Excessive investment of carbon in a root system might be at the expense of photosynthetic area and affect seed yield per plant. Some of the environmental variables that influence the relative size of shoots and roots include: photoperiod (day length), moisture stress, soil acidity, nutrient availability, shoot and root temperatures, diseases, insects, and plant population density (which affects intensity and spectral distribution of light received by the growing plants). The objective of this paper is to present some examples of light-mediated regulation of shoot/root relationships and to discuss how this can be relevant in plant-soil-water-light management.

MATERIALS AND METHODS

Photoperiod: Seedling-year biennial sweetclover (*Melilotus alba* Desr.) plants were observed for root development at monthly intervals under natural photoperiods from mid-August until mid-November in a field and in the soil bed of a greenhouse. Other plants were evaluated during growth in pots under long, short, and natural photoperiods in a warm greenhouse and outdoors.

Light Spectral Distribution: Effects of high or low FR/R light ratio on shoot/root biomass ratios of soybean (*Glycine max* L.) seedlings were determined in controlled environments. All plants were grown in the same growth chamber for about 23 hours and 50 minutes per day. All plants received 12-hour photoperiods at 520 μmol m^{-2} s^{-1} and day/night temperature of 25°C. At the end of each day for 20 consecutive days, plants received either 5 minutes of R, 5 minutes of FR, or 5 min FR followed immediately by 5 min R, as discussed by Kasperbauer (1).

The FR/R ratios in upwardly reflected light 10-cm above different colored soils and plant residues were measured at 5-nm intervals from 400 to 800 nm with a portable spectroradiometer. Black, brown, brick-red, tan and white soils were used. Measurements were taken over each soil color when dry, moist, or covered (80%) with plant residue. Similarly, measurements were taken 10-cm above artificially colored mulches. For plants grown over different colored soils the treatment apparatus was arranged so that roots were in containers suspended below insulation panels to maintain constant root temperature below the various colors. The plants grew through 2.5-cm diameter tubes that extended from the containers through the insulation panels and soil covers that were above the panels (2). Shoot and root characteristics were determined after 1 month of growth over the different colored surfaces.

RESULTS AND DISCUSSION

Light affects plant growth through photosynthesis and photomorphogenesis. The light-driven reactions of photosynthesis have been widely studied, and photosynthesis is the basis of many agronomic studies such as those involving leaf area index (LAI), canopy light interception, etc. Photomorphogenic light responses involve light receptors (such as phytochrome) that regulate how and where the new photosynthate is used within the growing plant. Under field conditions, both photosynthesis and photomorphogenesis are important determinants of plant growth, adaptation and survival.

Plants respond to photoperiod as an indicator of season, and to photosynthetic photon flux density (PPFD) and spectral distribution of light as detectors of competition from other plants. While photosynthesis regulates the amount of carbon fixed and biomass produced, photoperiod and spectral distribution of light regulate distribution (partitioning) of new photosynthate within the plant. Photoperiod plays a major role in shoot/root relationships in biennial plants; whereas, altered spectral distribution of light (as associated with plant population density) affects shoot/root relationships of most plants. Some examples are discussed below.

Photoperiod: Biennial sweetclover (*Melilotus alba* Desr.) provides an interesting example of a photoperiod-responsive legume that is usable for dinitrogen fixation and incorporation of organic matter into soils. The biennial growth habit is characterized by rapid shoot growth during the spring and early summer of the seedling year. During late summer and autumn, the shoot growth rate slows and roots enlarge rapidly as natural daylength and temperature decrease (3). At Ames, Iowa (42° N), Kasperbauer et al. (4) found that sweetclover taproot biomass increased rapidly from mid-August through mid-November. Relative to biomass in mid-August, taproot size had increased 2.3-, 3.1-, and 4.5-fold by mid-September, mid-October, and mid-November, respectively. Shoot size changed very little during that three-month period. Roots of plants grown on natural photoperiods in a soil bed in a warm greenhouse from mid-August until mid-November developed at the same rate as those exposed to natural low temperatures in the field during the same period (4). Those experiments demonstrated a dominant effect of photoperiod in the partitioning of relatively more photosynthate to roots of biennial sweetclover plants as days shorten in autumn.

In another experiment, Kasperbauer et al. (4) compared shoot/root biomass ratios of potted sweetclover plants that were grown from July 15 to November 15 in a warm greenhouse or outdoors under three photoperiods at Ames, Iowa. Shoot/root biomass ratios in mid-November are summarized in Table 1. The biomass ratios supported the concept that photoperiod played the major role in regulation of photosynthate partitioning in seedling-year biennial sweetclover plants. Within each tested photoperiod, the shoot/root ratios differed very little between plants kept in a warm greenhouse and those kept outdoors with naturally decreasing autumn temperatures. Plants growing on the shortest days produced low-growing, rosette shoot growth and enlarged taproots; whereas, plants on the longest days produced more shoot growth and much smaller taproots. The

TABLE 1. Shoot/Root Biomass Ratios of Biennial Sweetclover Plants Grown in a Greenhouse or Outdoors under 3 Photoperiods (Adapted from Reference 4).

Photoperiod and location*				
9-hour		Natural	24-hour	
Greenhouse	Outdoors	Outdoors	Greenhouse	Outdoors
0.36	0.35	0.47	3.72	3.78

*July 15 to November 15 at Ames, Iowa (42° N latitude).

first-year biennial plants apparently sensed photoperiod as an indicator of season, and the shoot/root responses to photoperiod served as an adaptation, or survival mechanism. That is, the biennial sweetclover used in those experiments had evolved to sense long days as a signal to partition more photosynthate to shoot growth (including flowers and developing seed) and less to root reserves because the life-cycle can be completed during the first year under very long photoperiods, and the plant dies after seed production. Thus, formation of a large root reserve would be counter-productive. On the other hand, the short photoperiod is sensed as autumn and the need to partition more photosynthate to storage taproots, which can support early growth, flowering and seed set during the following spring. The seasonal responses of biennial legumes to photoperiod are also very important in their use in soil improvement programs. Even though shoots may appear to stop growth during autumn months, the rapid enlargement of taproots is such that they continue to incorporate biomass until shoots freeze back for the winter (5). Realization of the photoperiodic regulation of shoot/root relationships should help maximize soil improvement benefits of a biennial legume by timing its incorporation as a green manure crop.

Light Spectral Distribution: Plants that are the same age and genetically identical can develop quite different shoot/root biomass ratios if grown in sparse versus dense populations, even if there is no nutrient or water stress. A plant growing in a dense population generally develops a longer stem, fewer branches, and a smaller root system relative to a genetically-identical plant growing in a sparse population. This growth pattern can occur in seedlings even before mutual shading decreases the amount of photosynthetic light. It is apparent that plants can respond morphogenically to some component of the environment that is influenced by population density. Further, it is apparent that the same component can initiatê events that result in partitioning relatively more photosynthate to shoots than to roots in high populations, and relatively less to shoots and more to roots in lower populations. The spectral distribution of light is a factor that varies with population density (1,6). Each green leaf absorbs most of the visible (photosynthetically active light, 400-700 nm) and reflects or transmits most of the far-red (FR) light (700-800 nm) (Figure 1). Thus, the amount of FR and the FR/R ratio received by a growing plant is influenced by the size, number and nearness of competing leaves. The FR/R photon ratio of light received by a growing plant affects the photoequilibrium level of photoreversible phytochrome within the plant (7), and initiates events that regulate partitioning of new photosynthate within the growing plant (6).

Controlled Environment: The effects of R and FR (and the FR/R ratio) on the shoot/root biomass ratio of seedlings grown in a controlled environment are shown in Table 2. Even though all plants had the same total light energy, the FR/R ratio for five minutes at the end of each day influenced the photoequilibrium level of the phytochrome system at the beginning of the night, and that level influenced partitioning within the plant to affect the shoot/root biomass ratio. The treatment in which FR was followed immediately by R resulted in partitioning patterns similar to those that received only R. This is interpreted as an indication that a R-FR photoreversible sensor (phytochrome) is present and functioning in initiation of events leading to photosynthate partitioning.

Spectral Distribution Affected by Competing Plants: Results of controlled environment studies and the fact that competing leaves can serve as FR-reflectors

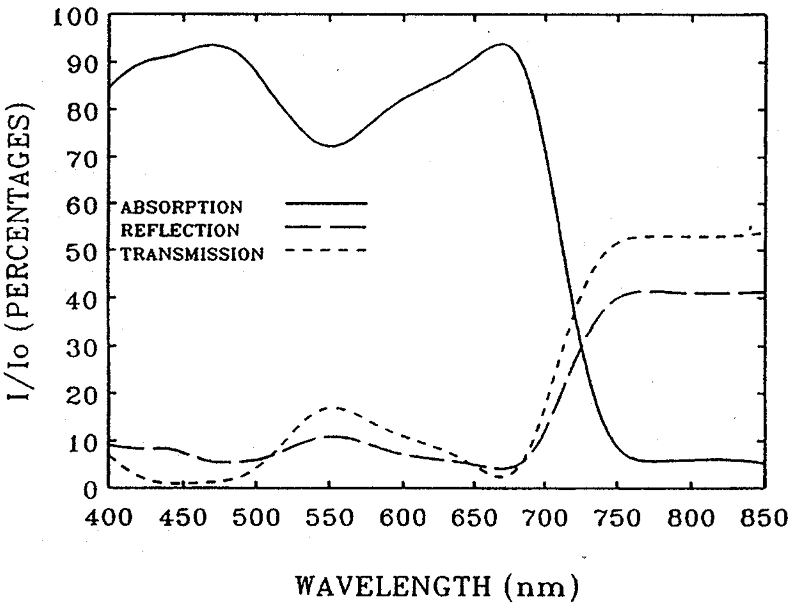

FIGURE 1. Absorption, Transmission and Reflection of a Typical Soybean Leaf. I/I_0 refers to light absorbed, transmitted and reflected at 5-nm intervals relative to incident light at the same wavelengths.

TABLE 2. Percentages of Dry Matter Partitioned Among Shoots and Roots of Soybean Seedlings Grown in a Controlled Environment with End-of-Day R (low FR/R ratio), FR (high FR/R ratio), or FR Followed Immediately by R Each Day for 20 Consecutive Days (Adapted from Reference 1).

End-of-day:		Dry biomass (%) in:		
Light	FR/R ratio	Shoots	Roots	Shoot/root ratio
R	Low	67.5	32.5	2.1
FR	High	76.8	23.2	3.3
FR,R	High,Low	66.2	33.8	2.0

(Figure 1) suggest that the FR/R ratio in the field should act through the phytochrome system to sense competition and to regulate various developmental events, including photosynthate partitioning and the shoot/root biomass ratio (1, 6). For example, a higher population of competing plants would result in more leaves reflecting more FR, causing a higher FR/R ratio and relatively more photosynthate partitioned to stems and less to roots. The longer stems would have the adaptive advantage of increasing the probability of keeping some leaves in sunlight.

Spectral Distribution Affected by Soil Surface Color: Several years ago it became apparent to us that crop yield responses to conservation versus conventional tillage (i.e. plant residue-covered versus bare soil) differed among geographic regions (8). In some regions crop yields were consistently better with conservation tillage (9). However, crop yields were often superior on bare soil in studies at the Coastal Plains Soil and Water Conservation Research Center at Florence, SC (10). After considering various environmental differences among the regions, we collected five different colors of soil from five different locations and measured spectra of upwardly reflected light when the soils were dry, wet and residue-covered. Spectra of upwardly reflected light (relative to the spectrum of incoming sunlight) are shown in Figure 2. The measurements were taken 10-cm above the soil surface because this is in the seedling establishment zone. Some interesting observations were evident. For example, the bare brick-red soil reflected little blue light (400-500 nm) and much in the R and FR regions of the spectrum. Reflection from the dark soils was increased by the plant residue cover; whereas, reflection from the light colored soils was decreased by the plant residue cover. The reflection spectra from the different colored soils with and without plant residue covers suggested that reflected light may contribute to different plant growth responses. To test this hypothesis, we grew soybean seedlings in containers that were suspended below styrofoam insulation panels that were covered with different colored soils in a greenhouse experiment (Table 3). The seedlings grew through 2.5-cm diameter tubes that passed from the soil

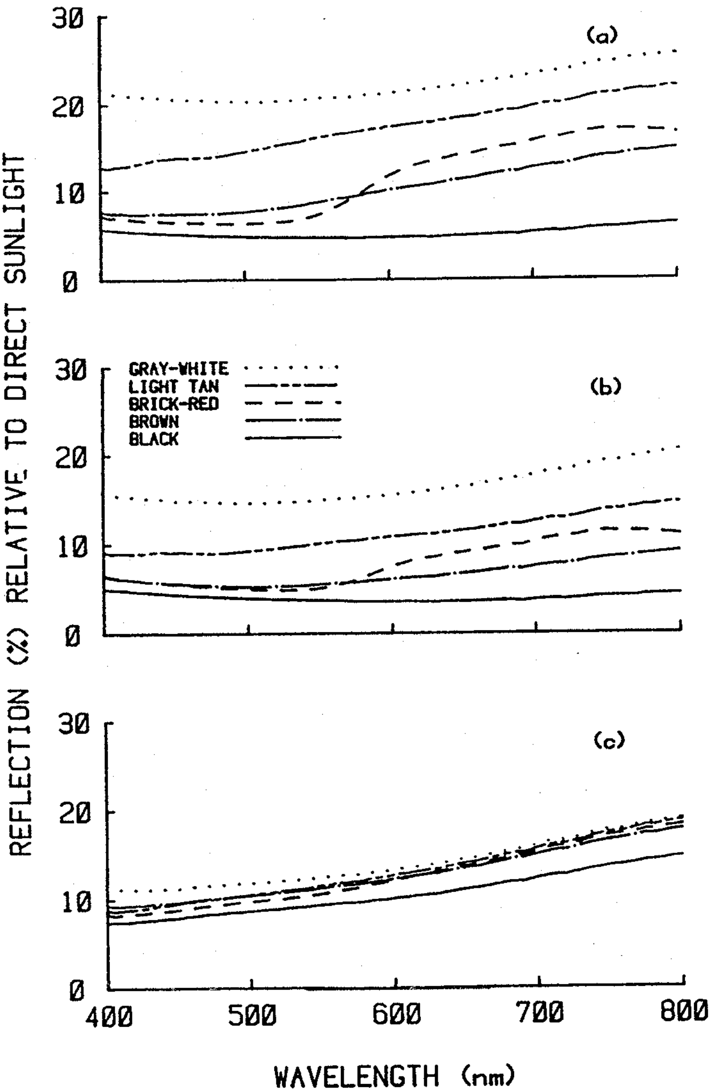

FIGURE 2. Spectral Distributions of Reflected Light 10 cm above the Variously Colored Soils Relative to Direct Sunlight (which was considered to be 100% for each measured wavelength) (a) Dry Surface, (b) Wet Surface, (c) Corn Residue-Covered Surface.

TABLE 3. Shoot and Root Growth and Nodule Characteristics of Soybean Seedlings Grown Over Different Colored Soils Covering Insulation Panels (Adapted from Reference 2).

Plant characteristic	Soil color			LSD
	White	Red	Black	(0.05)
Shoot				
Stem length, mm	127	138	141	14
Stem weight, mg	137	120	120	15
Root				
Tap weight, mg	38	38	39	NS
Lateral weight, mg	220	151	161	41
Total weight mg*	293	213	222	36
Root nodules				
Tap weight, mg	6	7	5	NS
Lateral weight, mg	29	17	17	11
Shoot/root ratio*	1.48	1.69	1.75	0.22

*Total root weight includes nodules, and total shoot weight includes leaves.

container through the insulation panels and soil cover. Because the soils were difficult to keep in place outdoors, other similar experiments were done using painted surfaces over insulation panels (Table 4). In both of these experimental approaches we were able to alter the spectrum of upwardly reflected light while removing the soil temperature variable by use of the insulation panels. An important observation was that plants growing over the white surface (either soil or paint) were shorter, had more root biomass and had lower shoot/root biomass ratios than plants grown over black surfaces (either soil or paint). An important finding was that soil surface color could alter the shoot/root ratio even when soil

TABLE 4. Shoot and Root Growth and Nodule Characteristics of Soybean Seedlings Grown Over Different Colored Insulation Panels (From Reference 2).

	Panel surface color			LSD
Plant characteristic	White	Red	Black	(0.05)
Shoot				
Stem length, mm	70	79	89	9
Stem weight, mg	83	79	66	NS
Root				
Tap weight, mg	37	28	25	8
Lateral weight, mg	160	135	110	49
Total weight mg*	242	195	157	76
Root nodules				
Tap, no.	8	8	7	NS
Lateral, no.	31	22	13	7
Tap weight, mg	16	17	13	NS
Lateral weight, mg	28	15	10	11
Shoot/root ratio*	1.51	1.74	1.86	0.28

*Total root weights include nodules, and total shoot weight includes leaves.

temperature was not a factor. Also, soybean seedlings that were inoculated with *Bradyrhizobium japonicum* developed more nodules and greater biomass of nodules when the plants were grown over the white surfaces.

The research into reflected light effects on morphogenesis over different colored soils and painted insulation panels was extended to high value horticultural plants grown over artificially colored plant residues and plastic mulches under field conditions. This approach has the advantage of allowing plants to grow in full sunlight for photosynthesis while using spectra of upwardly reflected light over the different soil surface colors (or colored mulches) to influence partitioning of the new photosynthate among plant components. Using this approach, we have altered shoot size, tomato fruit yield (11), and even concentration of the light harvesting chlorophyll protein of photosystem II (12). Other studies have been done to assess affects of colored mulches and upwardly reflected light on shoot/root ratios of root crops including turnip, radish and carrot.

CONCLUSIONS

Environmental factors contribute to expression of genes that regulate shoot/root relationships. Photoperiod and the spectral distribution of light received by a growing plant act through photomorphogenic pigments (such as phytochrome) within the plant to initiate regulation of many aspects of growth, development and productivity. Better understanding of naturally-occurring light-mediated regulation of shoot/root responses to light environment of the shoot will aid development of improved plant-soil-water-light management systems.

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